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# A phosphatized cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma, U.S.A.

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**Abstract.** **An exceptionally well-preserved cephalopod mouthpart was discovered in a phosphate concretion from the lower Missourian (Upper Pennsylvanian) in Tulsa, Oklahoma, U. S. A. It consists of an almost complete jaw apparatus and a radula, both of which are in the living orientation. The black upper and lower jaws, preserved as phosphate, were probably chitinous. The lower jaw is slightly larger than the upper and is characterized by a widely open outer lamella. The upper jaw is built up of a large outer lamella and a short, scallop-shaped inner lamella; the former is distinctly divided into two portions in the posterior region. The radula is preserved in the anterior portion of the buccal cavity; it is made of more than ten rows of teeth, each consisting of seven tooth elements with a pair of marginal plates. The overall features of the jaws and radula are essentially similar to those described in association with ammonoids rather than nautiloids and coleoids, suggesting that this mouthpart can be referred to the Ammonoidea. However, the lower jaw in our specimen differs from previously described mandibles of Carboniferous Gastrioceratoidea, Neoglyphioceratoidea, Gonioloboceratoidea, and Dimorphoceratoidea in its less elongate outline. For this reason, we refer the cephalopod mouthpart to the Ammonoidea other than the above superfamilies with reservation.**

**Key words: Ammonoidea, cephalopod mouthpart, Oklahoma, Upper Pennsylvanian**

## Introduction

All exatnt cephalopods possess a well-developed buccal mass in the proximal portion of the digestive system. The organic hard tissues of the cephalopod buccal mass consist of upper and lower jaws (beaks or mandibles) and a radula, all of which are surrounded by well-developed jaw-radular musculature. Fossilized remains of jaws and radula are rarely found in body chambers of ectocochliate cephalopod shells, especially of ammonoids and in the soft tissue remains of coleoids (see Tanabe and Fukuda, 1999, for a recent review). As Mapes (1987) has briefly documented, the marine Carboniferous in the U.S. Midcontinent occasionally yields goniatite conchs preserving jaws and a radula within their body chambers (Saunders and Richardson, 1979; Tanabe and Mapes, 1995; Doguzhaeva *et al.*, 1997). These goniatites occur in carbonate and phosphate concretions, together with occasional isolated cephalopod jaws and even more rarely radulae. In this article, an exceptionally preserved cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma is described and its possible taxonomic relationship is discussed on the basis of comparison with the jaws and radulae of extant and fossil cephalopods.

## Material and its geologic setting

The cephalopod mouthpart examined was preserved as a nucleus in a small spherical phosphate concretion (ca. 15 mm in diameter) that was recovered by one of us (RHM) from the Lower Missourian (Upper Pennsylvanian) on the southern side of Tulsa, Tulsa County, Oklahoma. The concretion came from an approximately 3 m thick stratigraphic sequence that consists of three distinct black platy shales that were exposed at the northeast corner of the junction of the 71st Street and the U.S. Highway 75 in the southern part of Tulsa, Tulsa County, Oklahoma (SW1/4, SW1/4, sec. 2, T. 18 N., R. 12E.: Supulpa 71/2 minute quadrangle; Figure 1). These shales were deposited in marine water under oxygen-stressed conditions that occurred during three distinct times of marine transgression and regression (Boardman, personal commun., 2001). The stratigraphic

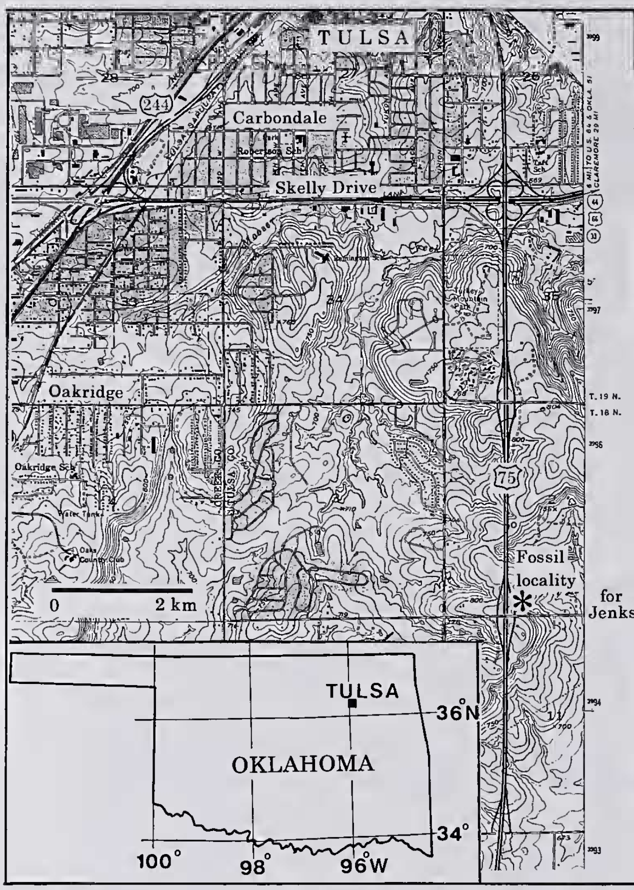



**Figure 1.** Index map of the southern part of Tulsa, Oklahoma, showing the locality of the cephalopod mouthpart remain examined.

assignment by Boardman *et al.* (1995, see localities OKM-28 and 56, p.86, although the reported coordinates they provide are incorrect) places these shale units in the lowest three cycles of the basal Missourian in the northern Midcontinent. All of the shales belong to the Coffeyville Formation, and the stratigraphic assignments for the three shale beds from oldest to youngest are the basal Tacket Shale, the lower Tacket Shale (= Mound City Member, Hertha Formation of Kansas) and the upper Tacket Shale (= Huspuckney Member, Swope Limestone of Kansas).

The exposure originally extended laterally for about 100 m and was covered by thousands of phosphate concretions that were eroding from the three black platy shales. Initial collections were made of the loose specimens on the surface without regard to stratigraphic position. In about 1990, prior to a field expedition to recollect and sample the exposure stratigraphically, the Oklahoma Highway Department of Transportation grassed the exposure, and it is not collectable at this time.

The cephalopod mouthpart specimen examined is housed in the Zoological Collection of Ohio University (OUZC).

## Notes on preservational conditions

It has been reported that some phosphate concretions from some Carboniferous Midcontinent black shales contain both mineralized skeletal material (bones and shells) and less commonly preserved softer organs (cephalopod mouthparts) of invertebrates (for mouthpart reports see Closs, 1967; Mapes, 1987; Tanabe and Mapes, 1995; Dogushaeva *et al.*, 1997). The reasons why and how phosphate preserves the soft tissue remains in this geologic setting has not been addressed. Because of the lack of *in situ* phosphate concretions from this Oklahoma locality, a detailed study of these specimens to solve the above problems is not warranted at this time. However, it is possible to make some general exterior and internal observations about the concretions from this exposure to help explain the preservation.

There are five concretion types classified on the basis of shape (flat and spheroidal) and on surface texture (smooth, rough, and bioturbated). The five concretion types are: 1) spheroidal with a smooth exterior, 2) flat with a smooth exterior, 3) spheroidal with a rough exterior, 4) flat with a rough exterior, and 5) bioturbated nodules which bear no body fossils. The cephalopod mouthparts that form the basis of this paper and most of the fossil material from this locality are preserved in the type 1 concretions. Although no systematic characterization of the nodule types was linked to the outcrop stratigraphy during initial collections in the early 1990s, the lowest shale (basal Tacket Shale Member) appeared to contain the most fossiliferous concretions.

The internal fabric of the concretions probably controls the surface texture and one of these fabrics lent itself particularly well to fossil preservation. Fecal pellets are common in these coprolite-dominated phosphate nodules. Both of the smooth-surfaced concretions (types 1 and 2) have a tightly packed, pelletal fabric without interstitial calcite cement; whereas, the two rough-surfaced types contain loosely

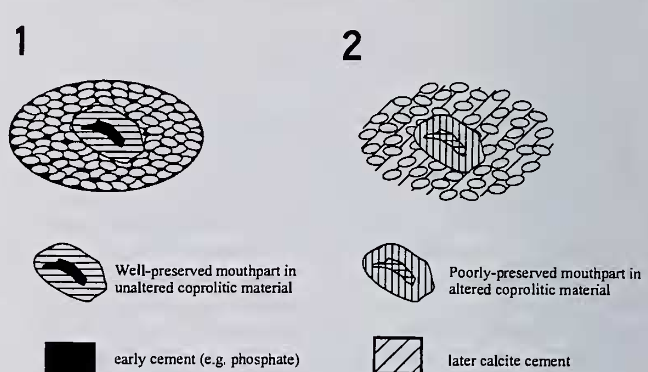



**Figure 2.** Schematic illustration of pelletal coprolites. **1.** Tightly packed pelletal fabric that was cemented early enough to favor high-quality fossil preservation. **2.** Calcite-cemented and loosely packed fabric that resulted in a rough surface exterior. Relatively poor fossil preservation characterizes these concretions probably because of later calcite cement that precipitated with infiltration of fluids that altered the coprolite and its enclosed fossils.

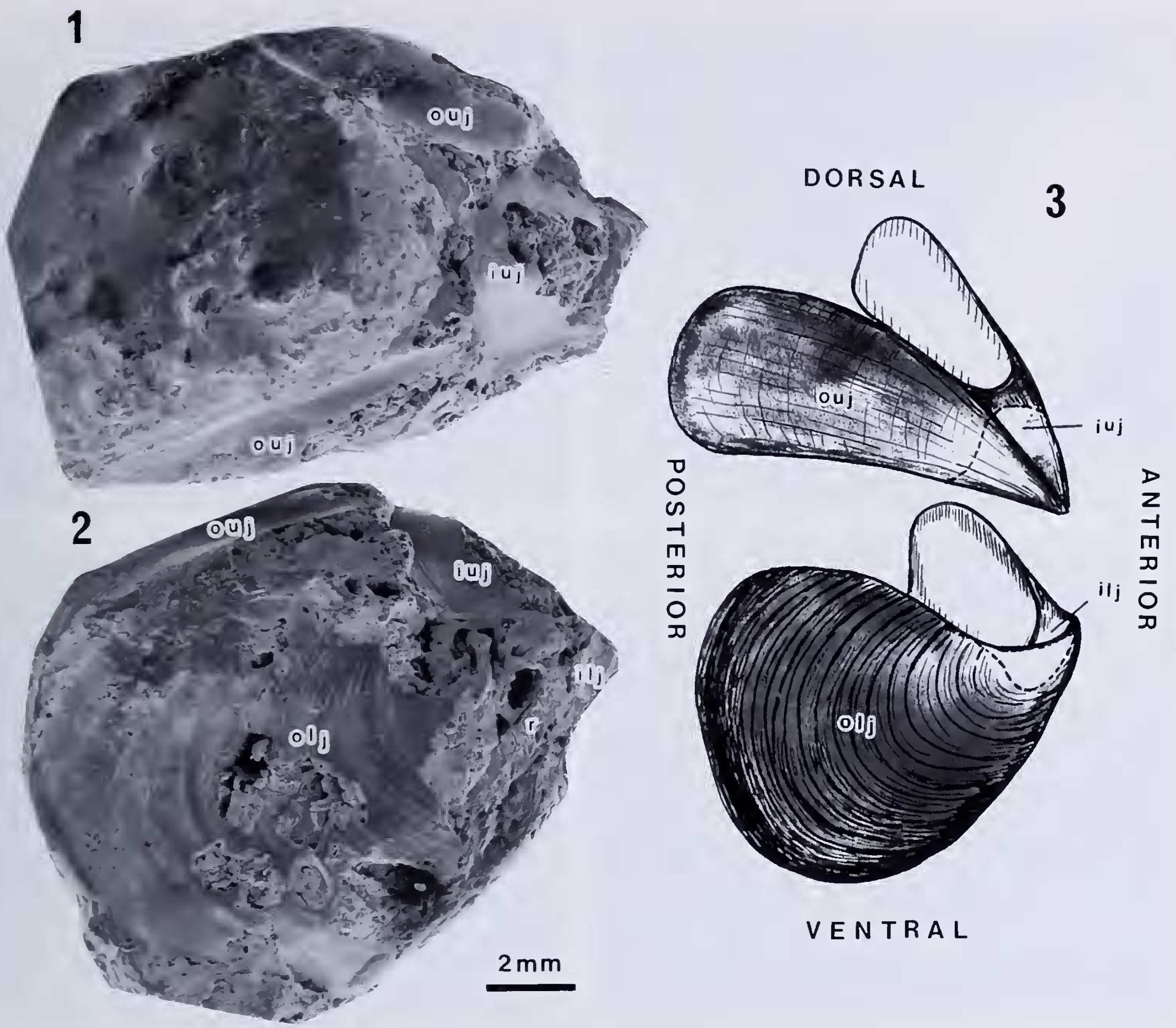


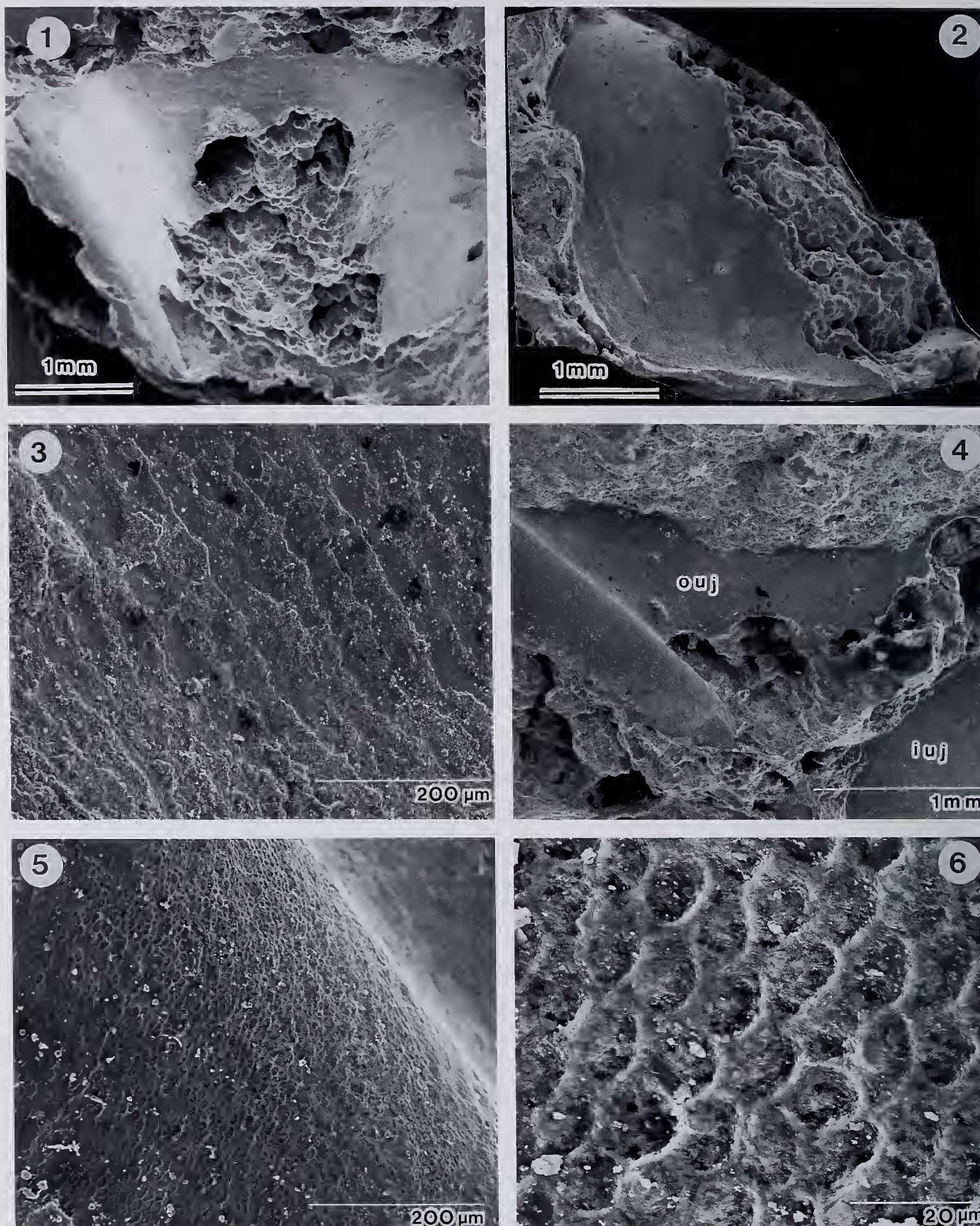

**Figure 3.** Dorsal (1) and left lateral (2) views of the phosphatized cephalopod mouthpart examined, and the reconstructed diagram of the jaw apparatus (anterolateral view) (3). Ohio University Zoological Collection, OUZC 4001. Abbreviations. ouj: outer lamella of upper jaw, iuj: inner lamella of upper jaw, olj: outer lamella of lower jaw, ilj: inner lamella of lower jaw, r: radula.

packed pellets and conspicuous interstitial calcite cement. The tight packing of pellets probably resulted in part from rapid, early diagenetic phosphate cementation of these concretions that sealed the concretions and favored high-quality fossil preservation by restricting entry of later pore fluids (Figure 2.1). Softness of pellets may also be a preservational factor, but analysis for that is beyond the scope of this report. The calcite cementation and loose packing of the rough concretions which contain poorly preserved fossils are interpreted as the result of infiltration of later diagenetic fossil-altering fluids (Figure 2.2).

Based on these observations, it seems apparent that the mode of phosphate and carbonate preservation will control some of the preservational potential of cephalopod mouthparts. However, detailed studies of carefully collected concretions will be required to resolve some of these preservational variables.

### Description of the cephalopod mouthpart

*Methods of observations.*—The cephalopod mouthpart from the Tacket Shale (Tacket specimen) was coated with platinum and examined by means of a Hitachi model S2400 scanning electron microscope. SEM images of the jaws and radula were transferred to a desktop computer via a PCI interface, and different portions of them were reorganized into a few images using imaging software (Quartz PCI and Adobe Photoshop, Ver. 5). They were printed out using a high-resolution digital photo-printer (Fuji Film Pictrography, model 3500).


1
1mm
2
1mm
3
200 µm
4
ouj
iuj
1mm
5
200 µm
6
20 µm

For determination of upper and lower jaws, we follow the criteria described by Lehmann (1976, 1990), Nixon (1988a, 1996), and Tanabe and Fukuda (1999), who relied upon the comparison with the jaws of extant cephalopods.

*Overall morphology.*—The Tacket specimen, of about 11.5 mm maximum length and 7 mm width, consists of an almost complete jaw apparatus and a radula (Figure 3.1, 3.2). The ventral margin of the upper jaw fits well with the dorsal margin of the lower jaw. The anterior portion of the lower jaw is partly eroded and/or corroded, and where the mandible is missing, a radular ribbon is exposed in the buccal cavity between the jaws (**r** in Figure 3.2). These observations indicate that the jaws and radula have been fossilized by keeping their original life orientation as a complete buccal mass.

*Upper jaw.*—The upper jaw is made of a black material which was probably originally chitinous. It consists of a large outer lamella and a short inner lamella, which are joined in the anterior portion; the former, though the anterior portion is missing due to weathering, is distinctly divided into two wing portions in the posterior region (Figure 3.1). The open angle of the wings is about 45°. The dorsal margin of the paired wing portions exhibits a sharp ridge-like elevation. This elevation can be traced to the anterior portion where two wing portions are connected by a slightly concave outer lamellar element (Figure 4.4). The inner shorter lamella is scallop-shaped and is prominently convex dorsally (Figure 4.1, 4.2). The anterior portion is partly missing, but the reconstructed outline suggests that this portion appears to be sharply pointed (Figure 3.3). The inner lamella is ornamented with dense concentric lirae (Figure 4.1–4.3). The outer lamella lacks growth lines and instead retains a delicate pattern represented by numerous honeycomb-like polygonal pits (Figure 4.5, 4.6). Each pit, about 8–12 μm diameter, is surrounded by a sharp ridge (Figure 4.6). In view of their shape and distribution, these pits are undoubtedly comparable to the anchor-type polygonal imprints of columnar cells (becublasts) that are present on the outer side of the upper jaw and on the inner side of the lower jaw in extant coleoids (Dilley and Nixon, 1976).

*Lower jaw.*—As in the upper jaw, the lower jaw is made of a black, probably originally chitinous material without any trace of a calcareous element. It is slightly larger than the upper jaw (Figure 3.2), and consists of a large outer lamella and a short inner lamella, though the inner one is partly visible from outside in the eroded anterior buccal cavity (**ilj**; Figures 3.2, 3.3). The two lamellae are connected to each other in the anterior portion. The outer lamella is curved posteriorly, with an open angle of about 50 degrees. Its outer surface is sculptured by regular-spaced, concentric undulations, which become finer and denser toward the posterior margin (Figure 3.2).

*Radula.*—The exposed radula comprises a total of 13 rows of teeth, retaining their original orientation. Each transverse row, about 2.5 mm wide, consists of seven tooth elements (a central rhachidian tooth, two paired lateral teeth, and a pair of marginal teeth), with a pair of marginal plates (Figures 5.1, 5.2). The shape of the rhachidian tooth is unclear because it is hidden by lateral teeth. The paired inner and outer lateral teeth are unicuspid, asymmetrical in frontal view and project markedly toward the anterodorsal side; the former is much shorter than the latter. The paired marginal teeth are the longest in the tooth elements and unicuspid as are the lateral teeth. The marginal plate has an oval outline.

## Taxonomic relationships

The isolated cephalopod mouthpart from the Tacket Shale exhibits several characteristic features including 1) a radula consisting of a total of seven tooth elements in each row, 2) an upper jaw being build up of a short, scallop-shaped inner lamella and a large outer lamella that is distinctly divided into two portions in the posterior region, 3) a lower jaw being made of a widely open outer lamella and a shortly reduced inner lamella, 4) absence of a calcareous jaw element, and 5) presence of coleoid-type polygonal imprints of beccublasts on the upper jaw lamella. These observations provide a reliable basis to infer the taxonomic relationship of the mouthpart owner by comparison with the radulae and jaws of extant and fossil cephalopods (Table 1). The upper jaw in our specimen is distinguished from those of extant coleoids and *Nautilus* in that the outer and inner lamellae of the latter are never divided into two wing portions (Clarke, 1986; Nixon, 1988a, b; Tanabe and Fukuda, 1999). Among the extant and fossil cephalopods, upper jaws with paired lamellae are only known from ammonoids (Tanabe and Fukuda, 1999, fig. 19.3). The three-dimensional architecture of the upper jaws of Goniatitina and Ceratitina is still unclear due to relatively poor fossil preservation. Bandel (1988, fig. 6) and Zakharov (1974, fig. 2B), respectively, reconstructed the upper jaws of the Upper Paleozoic goniatite (*Eoasianites*) and the early Triassic ceratite (*Olenekites*), as consisting of a widely opened, well-developed outer lamella and a short, reduced inner lamella. Later, Doguzhaeva *et al.* (1997) interpreted that the upper jaw of *Girtyoceras* (Carboniferous Goniatitina) is made of a large inner lamella and a short outer lamella, though they did not present an illustration showing this construction. The structure of the upper jaw in the Tacket specimen correlates well with the reconstruction of the upper jaws of goniatites and ceratites by Bandel (1988) and Zakharov (1974). Unlike the upper jaws of Goniatitina and Ceratitina, those of most Jurassic and Cretaceous ammonoids consist of a large inner lamella with paired lateral walls and a short, reduced outer lamella, though the two lamellae appear to be united as a single lamella in Late Cretaceous Ancyloceratina (e. g. *Jeletzkytes*;

← **Figure 4.** Upper jaw of the phosphatized cephalopod mouthpart examined. 1, 2: Anterior (frontal) (1) and right lateral (2) views of the scallop-shaped short inner lamella with concentric fine lirae. 3: Closeup of 2, showing the fine concentric lirae. 4. Part of anterior portion showing the outer lamella (ouj) with a strong lateral ridge and marginal portion of the inner lamella (iuj). 5. Outer surface of the left lateral portion of the outer lamella ornamented with numerous honeycomb-like imprints of beccublasts. 6. Closeup of imprints of beccublasts on the jaw plate, each surrounded by a sharp ridge.

1

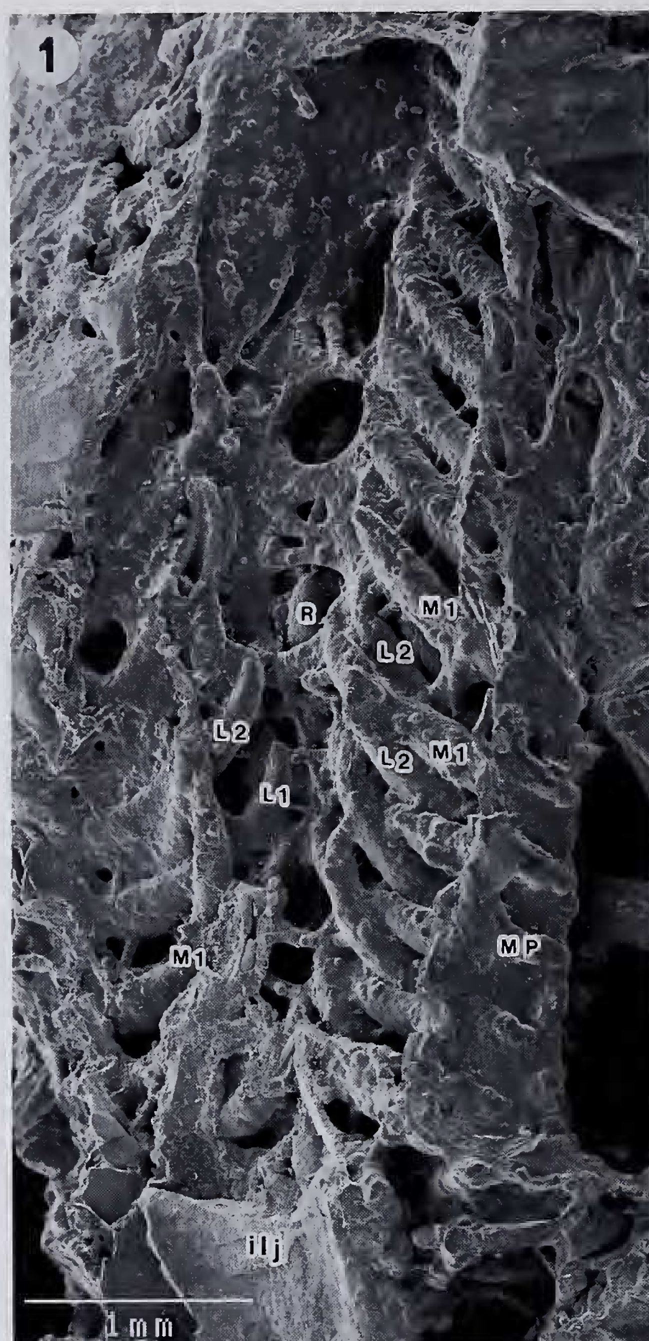



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**Figure 5.** 1. Anterior view of the radular ribbon preserved in the buccal cavity which is partly covered with the inner lamella of the lower jaw (ilj). 2. Diagram showing the frontal view of a transverse row of the radula. Abbreviations. R: central rachidian tooth, L1: inner lateral tooth, L2: outer lateral tooth, M1: marginal tooth, MP: marginal plate.

**Table 1.** Comparison of the morphological features of buccal structure in extant and fossil cephalopods (modified from Tanabe and Fukuda, 1999).

| Cephalopod taxa | Upper jaw elements | | Lower jaw elements | | | Beccublast imprints | Radular teeth in each row |
|---|---|---|---|---|---|---|---|
| | Rostrum | Lamellae | Rostrum | Inner lamella | Calcite cover | | |
| Recent *Nautilus* | calcified | non-divided | calcified | shortly reduced | partly present | micropores | 9 |
| Recent Coleoidea | non-calcified | non-divided | non-calcified | projected posteriorly | absent | polygonal pits | 7 |
| Ammonoidea | | | | | | | |
| Goniatitina | non-calcified | divided | calcified? | shortly reduced | absent | polygonal pits | 7 |
| Ceratitina | non-calcified | divided | non-calcified | shortly reduced | absent | unknown | unknown |
| Phylloceratina | unknown | unknown | calcified | shortly reduced | absent | unknown | unknown |
| Lytoceratina | unknown | unknown | calcified | shortly reduced | absent | polygonal pits | unknown |
| Ammonitina | non-calcified | non-calcified | non-calcified | shortly reduced | present or absent | polygonal pits | 7 |
| Ancyloceratina | non-calcified | non-calcified | non-calcified | shortly reduced | present | unknown | 7 |
| Present specimen | non-calcified | non-calcified | non-calcified | shortly reduced | absent | polygonal pits | 7 |

Landman and Waage 1993, figs. 37, 39–41; *Subptychoceras;* Tanabe and Landman, 2001, text-fig. 2. 6).

The lower jaw of the Tacket specimen is similar in the development of a large outer lamella to those of Upper Paleozoic Goniatitina such as *Eoasianites* (Neoicoceratoidea, Neoicoceratidae; Closs, 1967, fig. 4; Bandel, 1988, fig. 6), *Cravenoceras* (Neoglyphioceratoidea, Cravenoceratidae; Mapes, 1987, fig. 3.3, 3.4; Tanabe and Mapes, 1995, figs. 2-2, 3), *Wiedeyoceras* (Gonioloboceratoidea, Wiedeyoceratidae; Saunders and Richardson, 1979, fig. 7), and *Girtyoceras* (Dimorphoceratoidea, Girtyoceratidae; Doguzhaeva *et al.*, 1997, fig. 4), but in the latter, the outer lamellae are much more elongated posteriorly than in the former (we follow Bogoslovskaya *et al.*, 1999 for higher taxonomy of each genus). The lower jaw of an indeterminate goniatite (not *Girtyoceras limatum* as reported in Doguzhaeva *et al.*, 1997, fig. 2C, D) possesses a calcified rostrum, but such calcification has not yet been observed in the lower jaws of other Goniatitina and the Tacket specimen.

The radula in the Tacket specimen is allied to those of Goniatitina (e.g. *Eoasianites;* Lehmann, 1976, fig. 72; Tanabe and Mapes, 1995, figs. 2-4, 4-2; *Cravenoceras*; Tanabe and Mapes, 1995, figs. 2-3, 4-1; *Girtyoceras*; Doguzhaeva *et al.*, 1997, figs. 5A, 6A) in the number of tooth elements in each row and the overall shape of each tooth, though there are some variations in the relative length of marginal and lateral teeth. Also, polygonal imprints of beccublasts observed in the upper jaw of our specimen have been found on the upper jaw lamella of *Girtyoceras* (Doguzhaeva *et al.*, 1997, figs. 5B) as well as on the inside surface of the lower jaws of *Gaudryceras* (Cretaceous Lytoceratina; Tanabe and Fukuda, 1983, figs. 2, 3) and an unidentified aspidoceratid (Upper Jurassic Ammonitina; Tanabe and Fukuda, 1999, fig. 19.5D).

To summarize the above comparison, the overall features and structure of the jaws and radula in the Tacket specimen show an affinity to those described from the Upper Paleozoic Goniatitina, although, there is a marked difference in the lower jaw shape of the Tacket specimen and other described goniatite mandibles. Because of this difference in lower jaw shape, we refer the Tacket cephalopod mouthpart to the Ammonoidea and to a superfamily other than the Gastrioceratoidea, Neoglyphioceratoidea, Gonioloboceratoidea, and Dimorphoceratoidea with reservation.

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